ETHOLOGY OF EUDIOCTRIA TIBIALIS BANKS (DIPTERA: ASILIDAE) IN MARYLAND: PREY, PREDATOR BEHAVIOR, AND ENEMIES

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Abstract.—Eudioctria tibialis Banks foraged under bright skies from dimly lit or sunlit perches at temperatures above 16°C. Grooming, prey manipulation, feeding time prey prey, and foraging activities are discussed. Major prey were aphids and lower Diptera, although Isoptera or other insects were taken in large numbers when abundant. Most prey had thin cuticles and were weak fliers. Mean prey size was 3.02 mm. Females selected slightly larger prey than males. A list of prey is given. Vespula maculata (L.) may be an important predator of Eudioctria tibialis under certain conditions.

At the present time behavioral and ecological information on species of the genus *Eudioctria*, as well as most Asilidae, is limited. Scarbrough (1981) recently reported the seasonal distribution, abundance, and diurnal activities of a population of *Eudioctria tibialis* Banks in Maryland. Some biological information of several European species of *Dioctria* was contributed by Melin (1923) and Poulton (1906). However neither critically examined prey selection, but both concluded that *Dioctria* spp. selected primarily hymenopterous prey. The purpose of this study was to report on predator behavior and prey selection of *E. tibialis* and its enemies.

METHODS

General methods and location of the study site were described previously (Scarbrough, 1981). Data on predator behavior were obtained by censusing individuals at the study site and by following individual flies for extended periods. Hourly observations were made during the fly season to determine maximum variability in behavior patterns of predators and in the selection of prey types. During each census, flies were recorded as feeding or involved in other behaviors. Individual flies were observed in order to obtain information of foraging, feeding and manipulation behaviors. Prey were obtained by capturing feeding flies in a 15 dram snap top plastic vial, with the predator



Fig. 1. Male Eudioctria tibialis feeding on an aphid.

being released after the prey was dropped. Prey were later identified and measured from the front of the head to the tip of the abdomen for body length. Predator size was determined by taking similar measurements of 25 predators of each sex.

RESULTS AND DISCUSSION

PREDATOR BEHAVIOR

Eudioctria tibialis foraged under bright skies from dimly lit or sunlit perches at temperatures above 16°C. Asilids perched (N = 5095) horizontally on leaves and twigs of woody and herbaceous plants, overlooking an open space (Fig. 1). Foraging perches were invariably located 50 cm or more above the ground, although their heights varied considerably depending upon time of day and total sunlit area. Most foragers perched along the

vertical walls of the clearing during the early (N = 832, 81.0%; 1000–1300 hrs) and late (N = 1932, 52.0%; 1700–1900 hrs) observation periods and on the lower floor vegetation at other times (N = 2331, 70.0%; 1300–1700 hrs).

Eudioctria tibialis exhibited several behaviors while perching. The fly groomed ($\bar{x} = 9.3 \text{ min}$, N = 1092) its legs, wings, or head. This behavior was correlated with previous activities, e.g. facial and foreleg grooming followed feeding, abdominal and hindleg grooming followed copulation, and wing grooming followed unsuccessful foraging attempts and flights to new perches. Vertical and lateral head movements and body adjustments were also made in response to flying potential prey and other objects. Similar orientation response to flying objects have been described for other asilids (Scarbrough, 1978a, 1979; Dennis and Lavigne, 1975: Lavigne and Holland, 1969). Occasional wing flutters and short flights from perches occurred when flying objects moved near the flies. The fly responded to movement of insects or other arthropods, which shared a common perch, with lateral head movements. These were often followed by the fly moving away to another part of the perch or flying to another perch. The asilid was also induced to fly when flying objects came too close to the perch.

A fly may be induced to move to a new perch by other factors. *Eudioctria tibialis* often flew to new perches after a long period of inactivity although other arthropods did not induce the flight and atmospheric or sunlit conditions remained unchanged (Scarbrough, 1981). This behavior may be related to insufficient prey density. If this assumption is correct, this behavior had the advantage of exposing greater area and, thereby, increasing the probability of predator-prey contact. Similar observations have been reported for other asilid species (Lavigne and Holland, 1969; Hespenheide and Kubke, 1977; Scarbrough, 1979; Scarbrough and Sraver, 1979).

Foraging flights were short (R = 12–150 cm), with most prey captured within 80 cm (92%, N = 150) of perches. Absolute distances from perches to interception points of prey varied considerably with larger prey (>3.5 mm) being captured at greater distances than smaller prey, e.g. *Reticulitermes flavipes* (Koller) ($\bar{x} = 4.73$, N = 63) were captured within a range of 30 to 150 cm of perches whereas aphids ($\bar{x} = 1.5$ mm, N = 89) were captured within a range of 7 to 75 cm.

Flies often failed to capture an intended prey. In only 25.7% of the flights (N = 2843) were flies successful in capturing and feeding on prey. In some instances, prey were temporarily captured (5.2%) but were lost or released enroute to perches. Females were more successful (32.3%, P < .001) than males (17.3%) but males foraged less (P < .001) (Table 1). Perhaps this differential foraging behavior between the sexes is related to greater energy needs to accommodate a larger body and egg production in females (Scarbrough, 1978a, b, 1979).

This foraging behavior also differs from that of Cerotainia albipilosa Cur-

Time	Means (females)		Means (males)		
	Forage	Success	Forage	Succes	
10-1200	52.6	16.8	40.0	5.6	
12-1400	59.6	24.1	25.8	7.6	
14-1600	14.1	4.7	28.1	2.5	
16-1800	32.4	5.6	32.3	6.1	
.ĩ/fly/day	159.8	51.3	126.1	21.8	

Table 1. A comparison of foraging activity of male and female *Eudioctria tibialis* Banks per unit time. Data were obtained from observations of males and females during two hour units (N = 10). Data were compared with a 2 × 4 contingency table (χ^2).

ran (Scarbrough, 1978a, b, 1979) in that males of the latter species were more successful in capturing prey than females. It was suggested that lengthy courtship displays performed by males in front of non-receptive females disrupted the females' field of vision, and thereby interferred with their foraging behavior, resulting in a decrease in prey capture success. Females spent a significant amount of time discouraging courting males, e.g. threat postures and chasing, between forage flights (Scarbrough and Norden, 1977). Males of *E. tibialis* do not utilize courtship displays (Scarbrough, 1981), and perhaps the higher prey capture rates of females are related to less male disturbance.

General predator behaviors, e.g. flight patterns, methods of prey capture and immobilization of prey, and site of inserting the hypopharynx into soft and hard bodied prey utilized by *E. tibialis* were similar to those described for other asilid species (Scarbrough, 1978b; Scarbrough and Sraver, 1979; Scarbrough and Sipes, 1973; Dennis et al., 1978). It differed in that only large prey, such as termites, cicadellids, and reproductive ants, were manipulated in flight before returning to perches for feeding. Conversely, smaller prey were impaled upon the hypopharynx immediately upon capture. Flies returned to previous perches or flew to other perches to feed.

While feeding, the fly manipulated prey by "spinning" small prey, e.g. aphids, on its proboscis, using one foretarsus, or removing larger prey from its proboscis, then manipulating it and re-inserted the hypopharynx at a new location, using several tarsi. In the latter, most prey were manipulated with the fore- and hindtarsi while the midlegs and the end of the abdomen formed a "tripod" support of the body. The abdomen was arched down with its tip resting on a substrate.

Mating females usually manipulated prey as previously described, differing only in that their abdomens were arched less and did not rest on a perch. Additional support of the female's body was supplied indirectly by the union with the copulating male. One mating female manipulated a prey with its midtarsi while standing on its fore- and hindtarsi. The fly sometimes fell upon its pleuron where it manipulated large prey with six tarsi. Other manipulations included inflating the prey's body followed by abdominal pumping of the predator, and adjusting the depth of the hypopharynx in the prey. The latter was accomplished by resting the prey on a perch and forcing the hypopharynx deeper into the prey, or partially withdrawing the hypopharynx and forcing it into the prey again at a different angle. Tarsi were not used in these manipulations.

Feeding upon a prey was completed at a single perch unless the fly was disturbed. Following feeding, prey were usually discarded at perches by using one or both foretarsi or in flight while in pursuit of another prey. In the latter, one or both tarsi were positioned against the prey as the predator flew from the perch. A second or two later, the prey was observed falling through the air within a few cm of the perch. The prey is presumed to be pushed from the predator's mouth parts. The prey was sometimes discarded when the predator adjusted its hypopharynx in the prey's tissue. The prey while it lay on the perch. Tarsi were not used in this manipulation. Grooming of the head and foretarsi usually followed feeding.

Like most asilid species, the length of time *Eudioctria tibialis* spent feeding on a prey was variable, but correlated with prey size. The average feeding time per prey was 6.3 min (N = 21), ranging between 1 and 37 min. Small prey, e.g. aphids and psyllids, were fed upon for an average of 3.1 min (N = 128, R = 1-10 min) whereas larger prey, e.g. termites, were fed upon for an average of 20.9 min (N = 15, R = 13-37 min).

PREY SELECTION

The numbers, types, and sizes of prey taken by *Eudioctria tibialis* are presented in Table 2. Species of five insect orders formed the major components of the flies' diet, with Homoptera-Hemiptera being the most abundant. The predominant insect prey were aphids, termites, and lower Diptera in order of abundance. At least six other North American asilid species (Hespenheide and Rubke, 1977; Scarbrough and Sraver, 1979) take similar prey with aphids or Homoptera-Hemiptera forming the dominant segments of their diets. The proportion of termites in this sample is not viewed as significant as other prey because of their erratic and temporary appearance in the study area, but it does reflect the adaptability of the species to take advantage of temporary concentrations of prey. Of the prey taken occasionally, species of the orders Araneida (immatures), Thysanoptera, Psocoptera, and Lepidoptera formed less than 4% of the diet. Conversely, European *Dioctria* (Poulton, 1906; Melin, 1923) select predominantly Hymenoptera.

Mean size of all prey was 3.02 mm, ranging from 0.81 to 6.46 mm in body length (Table 2). Specimens of Homoptera-Hemiptera, forming the major

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Table 2. Prey of *Eudioctria tibialis* Banks in Maryland. Predator size (N = 25 per sex): $\Im \Im x = 9.56 \pm 0.54$, R 8.5–10.5 mm; $\Im \Im x = 8.67 \pm 0.57$, R 7.0–9.6 mm. Mean size compared by Student's t-test.

Taxa	Total	<i>%</i>	Measured	(mm) ¹	± S.D.	Range (mm)
Diptera	81	17.5	59	2.49	1.38	1.00-5.10
Coleoptera	43	9.3	33	2.52	0.59	1.34-3.74
Isoptera	93	20.1	89	4.73	1.48	1.48-6.46
Homoptera-Hemiptera	179	38.7	130	1.98	0.93	1.10-5.05
Aphididae	148	32.0	75	1.52	0.50	1.25-2.75
Others	31	6.7	25	3.37	1.53	1.10-5.05
Hymenoptera	51	11.0	42	2.89	1.35	1.36-6.08
Miscellaneous	15	3.2	11	3.14	1.91	0.81-5.40
	462	99.8	364	3.02	1.13	0.81-6.46

¹ Prey means compared by Newman-Keuls multiple range test.

prey items in the flies' diet, were significantly smaller (P < .001; Newman-Keuls multiple range test) than other prey. Furthermore, prey in all orders except Isoptera were small, with over 80% less than 4.0 mm in total length. Isoptera were significantly larger (P < .001) while Hymenoptera, Coleoptera, and Diptera (P < .001) followed in decreasing size order.

Female predators were larger (P < .001; Student's t-test) than males and took slightly larger prey ($\bar{x} = 3.15 \text{ mm } 99$, N = 176, $\bar{x} = 2.72 \text{ mm } \delta\delta$, N = 286; P < .05) although both sexes took prey in all sizes. Males took proportionally fewer termites ($16.2\% \delta\delta$, 23.2% 99) than females. Selectivity of prey is partly based upon predatory-prey size. In the latter, termite swarms occurred when male *E. tibialis* was involved in other behaviors, e.g. searching and mating (Scarbrough 1981), and thus the proportion of termites in the male's diet may reflect termite availability rather than size discrimination. Predator-prey ratios were 3.2 and 2.9 for females and males, respectively.

The proportion of prey types in the diet of some asilids change in time and space. This phenomenon is related to differential activity periods of different prey taxa (Hespenheide and Rubke, 1977; Scarbrough, 1979; Scarbrough and Sraver, 1979; Powell and Stage, 1962). Similar results were apparent in the diet of *E. tibialis* in which swarming termites and ants were captured during short periods of a few days during the study. No significant change ($P \sim .05$) occurred in prey composition among other major taxa, although some species, especially aphids (Dixon, 1973), have a diurnal unimodal or bimodal flight periodicity.

It is generally accepted that asilid predator success is based partly upon flight capabilities and sizes of the fly and its potential prey. Small weak flying prey will invariably be vulnerable to larger, stronger, more agile predators (Hespenheide, 1975). Most prey of *E. tibialis* were small, about onethird the predator's size, and weak fliers. These prey, especially aphids, utilize convection currents to carry them into the air and subsequently back to ground level (Dixon, 1973). Furthermore, weak fliers usually have soft or thin cuticles. Examination of these prey for punctures revealed that any location on the prey's body may be penetrated by the hypopharynx although the dorsum contained the greater proportion (67%, N = 153) of punctures. Conversely, some larger prey with hard cuticles, e.g. reproductive ants and beetles, were immobilized by inserting the hypopharynx at specific locations of the body where the cuticle was thin or soft. Therefore, size of prey may be less limiting when weak flight abilities and thin or soft cuticles co-exist, e.g. termites.

The following is a list of prey taken by *E. tibialis* at the study site. A few prey are presented only to order or family level since they were too damaged for identification or were not collected. Each notation of prey refers to a single record unless followed by a number in parentheses. The month and year are recorded only once at the end of a series for each prey taxon.

ARANEIDA: Unidentified 14.V1.73. ISOPTERA: Rhinotermitidae, Reticulitermes flavines (Kollar) [4(2),21,23(12),25(8),26(3),27(3),28(2),30(8),V1.75, 7.V11.73, 30(17).V1.74, 18.23.24(3).26(2).28(1).V1.76. PSOCOP-TERA: Caecilidae, Caecilus aurantiacus (Hagen) 27.V1.74; Lachesillidae, Lachesilla pallida (Chapman) 29.V1.74; Psocidae, Blastopsocopis lithinus Chapman 27.VI.73. THYSANOPTERA: 19.VI.74, 8.VII.74, 7.VII.75, 26.27(2).28(3).VI.76; Thripidae, Ctenothrips bridwelli (Franklin) 27.VI.73. HOMOPTERA-HEMIPTERA: Aphididae, unidentified 3.VII.72, 15.29.VI.75, 5.7(6). 8(4).10(2).VII.75, 16(3).24(3).26(4).27(5). 28(15).29(6).VI.76, 5(2).10.VII.76, Acyrthosiphon solani (Kaltenbach) 28.V1.73, A. dirhodum (Walker) 5.V11.74, Amphorophora spp. 13(3).18(2). 29(3). VI.74, Anoecia corni (Fabricius) 14. VI.74, Aphis spp. 19(3). VI.73, 3(2). VII.74, A. fabae Scopoli 29(2). VI.74, A. gossypii Glover 19(2). 29. VI.73, A. rumicis Linnaeus 23.VI.73, A. sambucifoliae Fitch 23.24(2).VI.73, 27.30.V1.74, 10.V11.74, Cavariella aegopodii (Scopoli) 27.29.V1.74, Dactynotus sp. 20.VI.73, 18.VI.74, D. tisserti (Boudreaux) 19(2).VI.73, Eriosoma sp. 20.VI.73, E. lanigerum (Hausmann) 12(2).VII.74, Hyadaphis ervsimi (Kaltenbach) 3.VII.74, Macrosiphum spp. 19.29(2).VI.73, 23. VI.74, 5(2). VII.74, M. avenae (Fabricius) 20(2). VI.73, 20. VI.74, M. corvli Davis 9.VII.74, M. liriodendri (Monell) 25(4).26(3).29(2).30(3).VI.73, 20(2).VI.74, 1.VII.74, Megoura sp. 27.VI.73, Myzus sp. 3.VII.72, 13(10).28(2).VI.73, M. cerasis (Fabricius) 13.VI.73, Ovatus phyloxae (Samson) 28.30(9). VI.73, 17(3). 18.19. VI.74, 12. VII.74, Pemphigus sp. 24.27. VI.73, Rhopalosiphum fitchii (Sanderson) 27.VI.74, R. padi (Linnaeus) 27.30.VI.74, Sitomyzus sp. 18.21.23.V1.74, S. rhois (Monell) 23(2).V1.74, Thecabius sp. 22.V1.73, Therioaphis sp. 18.V1.74, T. riehmi (Börner) 30.V1.74, Tinocalis carvaefiliae (Davis) 21.VI.73, Toxoptera viridirubra Gill and Palmer

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27.VI.74; Cercopidae, Clastoptera obtusa Say 20.VI.73; Cicadellidae, Aphrodes sp. 30(2).VI.74, Dikraneura sp. 23.V1.73, Doratura stylata (Boheman) 20.VI.73, Empoasca fabae (Harris) 27.VI.73, Endria inimica (Say) 15.VI.73, Erythoneura sp. 23.VI.73, 18.VI.74, Forcipata lica DeLong and Caldwell 20.V1.74, Macrosteles sp. 30.V1.72, M. fascifrons (Stål) 14.V1.73; Cydnidae, Pangaeus bilineatus (Say) 29.V1.74; Miridae, Halticus bractatus Say 22.V1.73, Lygus sp. 21.V1.74, Lygidea medax? Reuter 13.V1.73, Trigonotylus tarsalis (Reuter) 14.V1.73; Phylloxeridae, unidentified 8.VII.75, 24(2).27(2).VI.76, Phylloxera sp. 3.VII.74; Psyllidae, Trioza diaspyri Ashmead 21.V1.74. COLEOPTERA: Unidentified 17(4).8(2).75; Anobiidae, Petalium sp. 26.V1.73, 14.VI.74; Chrysomelidae, Chaetosoma sp. 15.23.VI.73, 19.VI.74, Hippariphila sp. 20.VI.73, Paria sp. 22.25.VI.73; Curculionidae, Anthonomus sp. 20.VI.73, Dryophthorus americanus Bedel 21(2).26.VI.73; Scarabaeidae, Ataenius imbricatus (Melsh) 26.VI.73; Scolytidae, Orthotomicus caelatus (Eichhoff) 20(3).21(2).V1.73, Delphastus pusillus (LeConte) 27.VI.74, 26.VI.75, 8.VII.75; Staphylinidae, unidentified 3(2).14.VII.73, 14.19(2).20.21.26(4).VI.73, 19(2).26.29(2).30(2).VI.74, 2.3.4(2).VII.74. DIPTERA: Unidentified 19.VI.73, 6(2).8(2).15.27.V1.75; Agromyzidae, Cerodontha dorsalis (Loew) 21.VI.74, Liriomyza sp. 24.V1.73; Asilidae, Cerotainia albipilosa Curran 9.V11.73; Cecidomyiidae, unidentified 23.V1.73, 14.V1.74, 27.V1.75, 29.V11.75, Asynapta (s.l.) sp. 14.V1.73, Resseliella sp. 20.VI.74; Chironomidae, Orthocladiinae 7(2).14.VII.72, 20.22.30.BI.73, 17.21(2).23(3).VI.74, 1.3.VII.74; Chloropidae, Chlorops obscuricornis Loew 15.V1.73, Elachiptera costata (Loew) 15.V1.73, Oscinella carbonaria (Loew) 29.V1.74, Stenoscinis longipes (Loew) 25.VI.73; Dolichopodidae, unidentified 3(2).10.VII.72, 26.V1.75, Chrysotus sp. 3(2).10.VII.72, 14.15.20.VI.73, Condylostylus sp. 13.VI.73, Gymnopternus sp. 15.V1.73; Drosophilidae, Scaptomyza pallida (Zetterstedt) 1.VII.73, 29(2).VI.74; Empididae, Euhybus purpureus (Walker) 18.VI.74, Lactistomyia insolita Melander 9.VII.73, Platypalpus sp. 14. V1.74; Lauxaniidae, Homoneura philadelphica (Macquart) 13.15.V1.73. 18.VI.74; Milichiidae, Neophyllomyza sp. 17.VI.74, unidentified 26.VI.74; Phoridae, Megaselia sp. 3.VII.74; Platystomatidae, Rivellia pallida Loew 23.VI.73; Platypezidae, Platypeza sp. 3.VII.72, 20.VI.73; Rhagionidae, Rhagio mystaceus (Macquart) 18. VI.74; Sciaridae, Bradysia sp. 13. VI.72, 22(2).24.26(2).29.30(2).V1.73, I.V11.73; Sphaeroceridae, Leptocera sp. 10. VII.72, 20. VI.73; Stratiomydae, Oxycera sp. 20. VI.73; Syrphidae, unidentified 5.VII.75; Tephritidae, unidentified 3.VII.72; Tipulidae, unidentified 10.VII.72, 29.VI.73, Atarba picticornis Osten Sacken 24.25.VI.73, Dicranoptycha sp. 20.V1.73, Cheilotrichia stigmatica (Osten Sacken) 26.V1.73, Limnophila sp. 22.V1.73, Molophilus sp. 29.V1.73, LEPIDOP-Unidentified 19.VI.74. HYMENOPTERA: Unidentified TERA: 13(2).21(2).VI.73, 27(3).VI.76; Aphidiidae, Aphidius sp. 19(2).VI. 73, Lysiphlebus sp. 2.VII.74, Trioxys sp. 22.VI.73; Braconidae, unidentified 28. VI.76, Apanteles sp. 27.VI.73, Opius spp. 20(2).22.VI.73, Meteorus sp. 29.VI.73; Ceraphronidae, Ceraphron sp. 22.VI.73, 18.VI.74; Megaspilidae, Megaspilus sp. 24.VI.73; Chalcidoidea, unidentified 30.VI.73; Cynipidae, unidentified 24.VI.73; Diapriidae, Belyta sp. 25(2).VI.73, Pantoclis sp. 20(2).VI.73, Psilus sp. 28(4).VI.73; Dryinidae, Anteonini 14.VI.73; Eupelmidae 17.VI.74; Eurytomidae, Harmolita sp. 15.VI.73; Formicidae, Ponera sp. 27.28(2).VII.76; Hybrizontidae, Hybrizon rileyi (Ashmead) 25.VI.73; Ichneumonidae, Endasys sp. 15.VI.73, Polyaulon sp. 13.20(3).23.26(3).VI.73, Theroscopus sp. 20.VI.73; Pteromalidae, Lamprotatini 20.VI.73, 11.VI.74, Pteromalini 29.VI.74; Scelionidae, Calotelea sp. 14.VI.73, Trisacantha sp. 17(2).VI.74; Tenthredinidae, Ametastegia recens (Say) 20.VI.73.

PREDATORS OF EUDIOCTRIA TIBIALIS

Predaceous arthropods, especially other insects, have been recorded as enemies of asilid flies (Hull, 1962; Lavigne et al., 1978). Some common predators of adult asilids are spiders (Bromley, 1914; Scarbrough, 1978b, 1979), other asilids and conspecifics, e.g. cannibalism, and Hymenoptera (Hull, 1962; Lavigne et al., 1978; Scarbrough, 1978b, 1979). Eudioctria tibialis has similar enemies but differs in that cannibalism was absent and a new predator, Vespula maculata (L.) (Hymenoptera: Vespidae), was identified. At least 46 attempts at predation and 23 instances of predation were observed: Araneida (7), Laphria sicula McAtee (1) (Diptera: Asilidae), and V. maculata (15). In addition, eleven carcasses of E, tibialis were found. each with a crushed thorax and missing body parts. Vespula maculata was probably the predator since it typically mutilates the prey's body as the prey is being immobilized. The wasp crushed the prey's body and removed the wings with its mandibles bofore flying away with the remainder. Similar immobilization techniques have been reported for the wasp with other prey (Howell, 1973). Sometimes the prey was dropped as the wasp flew away. Three ants (Formica subsericea Say) were observed carrying carcasses of *E. tibialis.* The ants may have found the adults emerging from pupal cases (personal communication, D. S. Dennis, June 1980). Because of the similarity of the crushed bodies with those taken from feeding V. maculata and the absence of pupal cases in the study area, it is doubtful that the ants were the predators, but probably found them after they were dead.

Acknowledgments

l express appreciation to the following authorities at the Systematic Entomology Laboratory, USDA, Beltsville, Maryland, and Washington, D.C., for identifying most of the prey of *E. tibialis*: R. D. Gordon (Scarabaeidae); D. R. Smith (Formicidae, Tenthredinidae, Isoptera); L. M. Russell (Aphi-

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didae, Phylloxeridae, Psyllidae); J. P. Kramer (Cicadellidae, Cercopidae); J. L. Herring (Miridae); A. S. Menke (Vespidae, Cynipoidea); G. Gordh (Eupelmidae, Pteromalidae, Eurytomidae); B. D. Burks (Chalcidoidea); P. M. Marsh (Aphidiidae, Braconidae, Ceraphronidae, Dryinidae, Megaspilidae, Diapriidae, Hybrizontidae, Scelionidae); R. W. Carlson (Ichneumonidae); R. W. White (Anobiidae, Chrysomelidae); D. M. Anderson (Curculionidae, Scolytidae); J. M. Kingsolver (Staphylinoidea); C. W. Sabrosky (Chloropidae, Milichiidae); R. H. Foote (Tephritoidea); G. C. Steyskal (Agromyzidae, Dolichopodidae, Platystomatidae, Sphaeroceridae, Lauxaniidae); F. C. Thompson (Tipulidae, Syrphidae); L. V. Knutson (Empididae); R. J. Gagné (Cecidomyiidae, Sciaridae); and W. W. Wirth (Rhagionidae, Drosophilidae, Phoridae, Platypezidae, Stratiomyidae, Chironomidae). Identifications were also provided R. C. Froeschner (Cydnidae) and D. R. Davis, Department of Entomology, Smithsonian Institution, Washington, D. C.; E. L. Mockford (Psocoptera), Department of Zoology, Illinois State University, Normal; and W. B. Peck (Araneida), Department of Biology, Central Missouri State College, Warrensburg, I identified the Asilidae. Erik Scully, Department of Biological Sciences/Institute of Animal Behavior, Towson State University, provided assistance with the statistical analyses and read a preliminary draft of the manuscript. L. V. Knutson, Chairman, Insect Identification and Beneficial Insect Identification Institute, USDA, Beltsville, Marvland, and D. S. Dennis, Stearns-Roger Corp., Denver, Colorado, examined a revised draft of the manuscript. Thanks are also expressed to the Faculty Research Committee, Towson State University for grants that supported this study.

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